

Selective Predation and Prey Location in the Sea Slug *Navanax inermis*

BY

GREG M. BLAIR AND ROGER R. SEAPY

Department of Population and Environmental Biology, University of California, Irvine, Irvine, California 92664

(2 Text figures; 1 Map)

INTRODUCTION

THE SEA SLUG *Navanax inermis* (Cooper, 1862) occurs on low littoral and shallow sublittoral bottoms and is known to be a voracious predator on opisthobranch mollusks (RICKETTS & CALVIN, 1968). The prey preferences of *N. inermis* from a sandy bottom bay and an exposed rocky coastline were studied by PAINE (1965) at San Diego, California. In both environments the most abundant species of opisthobranchs (*Bulla gouldiana* Pilsbry, 1893 in the bay and 3 species of nudibranchs on the rocky coastline) represented the dominant components of *N. inermis*' diet. However, prosobranchs were conspicuously absent from its diet, and PAINE (1963) observed that *N. inermis* would not ingest the prosobranchs *Conus californicus* Hinds, 1844, *Nassarius tegula* (Reeve, 1853), or *Olivella biplicata* (Sowerby, 1825).

On the mud-sand bottom surrounding Balboa Island at Newport Beach, California, *Navanax inermis* is a common and conspicuous macroinvertebrate. In this environment, available gastropod prey include the opisthobranchs *Haminoea virescens* (Sowerby, 1833) and *Phyllaplysia taylori* Dall, 1900, and the prosobranch *Nassarius tegula*. If *N. inermis* selects opisthobranch prey in proportion to their abundance in the environment, *N. inermis* occurring at Balboa Island should preferentially feed on *H. virescens* and *P. taylori*.

Chemoreception is known to exist (KOHN, 1961) in a variety of gastropods. Distance chemoreception has been demonstrated in several nudibranchs (STEHOUWER, 1952; BRAAMS & GELEN, 1953) and in the neogastropod *Conus* (KOHN, 1959). However, *Navanax inermis* actively tracks and captures its prey by contact chemoreception. Unlike the nudibranch *Dirona albolineata* MacFarland, 1912, which appears to locate prey by direct chemoreceptive contact (ROBILLIARD, 1971), *N. inermis* locates its prey by

first recognizing the presence of an acceptable prey mucus trail, and then following that mucus trail to its producer. MARCUS (1961) showed that *N. inermis* has two chemoreceptive areas located on either side of its head and that it characteristically follows the mucus trails of its prey by placing one or both of these areas directly on the mucus trail. It then simply follows the trail, overtakes, and then ingests the prey. This predatory behavior pattern permits the experimental manipulation of predator and prey. For example, PAINE (1963) guided *Bulla gouldiana* (a known prey type of *N. inermis*) in a figure nine pattern, but stopped the animal just before completing the circular portion of the number. When following the trail from the base of the figure nine pattern, *N. inermis* would pass *B. gouldiana* by only 2 cm, but would not deviate from the trail. Instead it followed the figure nine to where the *B. gouldiana* stopped. In the present study, variations on this experimental approach were executed by manipulating various prey types along the prescribed mucus pathways or along pathways comprised of the mucus trails of different prey types. *Navanax inermis* was then placed in the vicinity of each trail and its movements observed and recorded.

MATERIALS AND METHODS

During April to June of 1971 *Navanax inermis* was observed and collected on the eastern shore of Balboa Island, Newport Beach, California (Figure 1) either above or near the low water mark. Specimens were observed on mud bottoms in the proximity of *Zostera marina* Linnaeus, 1753, or occasionally within the eelgrass itself. Individuals used in the food preference study were collected as they were encountered in the field and retained in 1-gallon capacity buckets for an average of 48 hours and allowed to

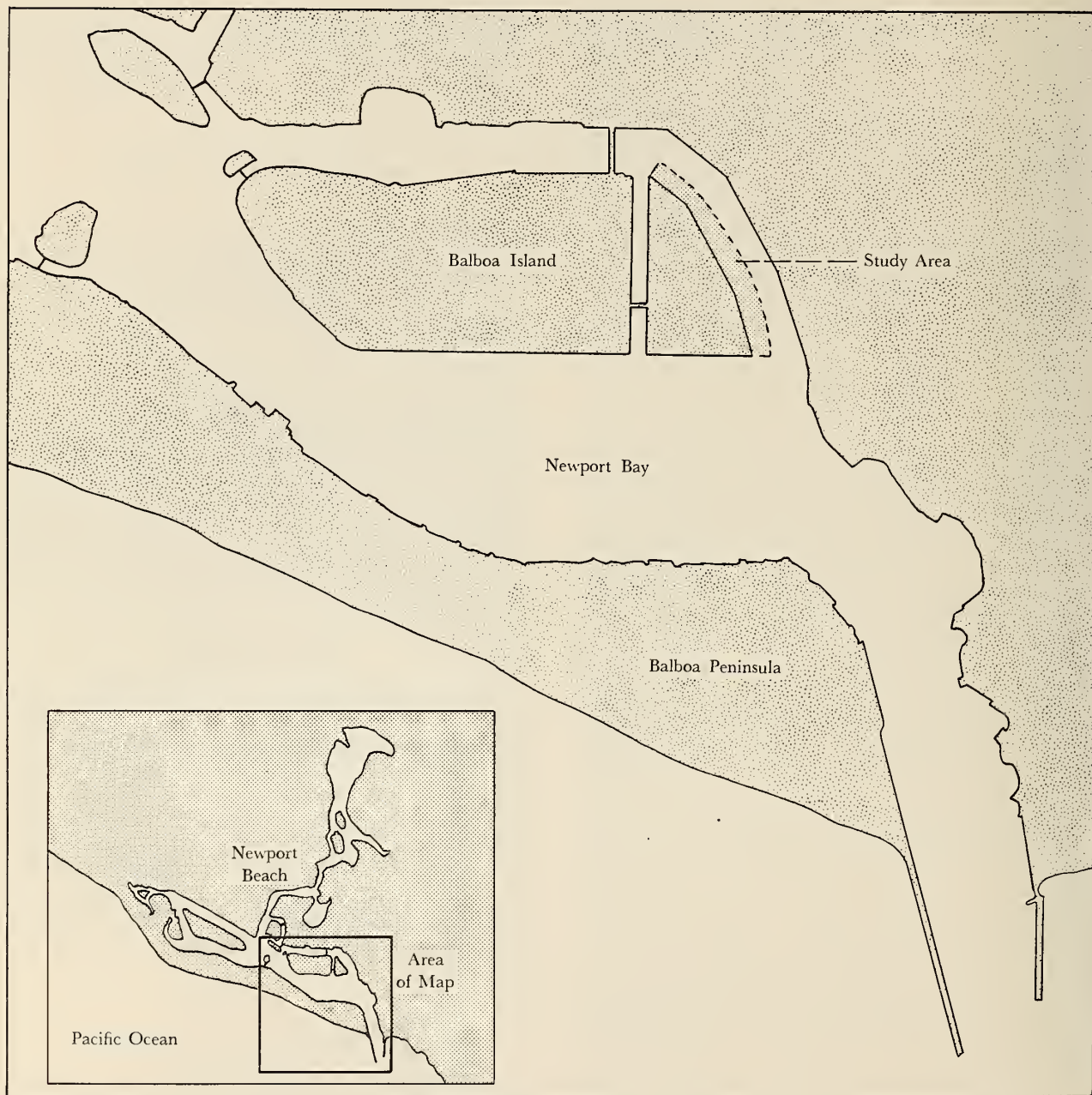


Figure 1

Location of study area on Balboa Island, Newport Beach, California
at 33°36'20" N latitude, 117°53'10" W longitude

defecate any hard parts. This period of time was quite adequate since in the study by PAINE (1965) only 20 to 30 hours were normally required for *N. inermis* to clear its gut. The buckets were kept in a shaded outdoor closet

at temperatures that ranged from 18.0 to 20.7°C. The sea water in each bucket was replenished daily.

Two areas of beach were selected to estimate the local abundance of the possible prey types of *Navanax inermis*

Table 1
Gut Content Analyses of *Navanax inermis*

Weight of <i>N. inermis</i> (g)	Time of day	Prey defecated	Prey length (mm)
10.5	Afternoon	None	
10.8	Afternoon	None	
11.5	Afternoon	<i>Haminoea virescens</i>	5
11.8	Afternoon	<i>Teinostoma supravallatum</i>	2
12.0	Morning	<i>Haminoea virescens</i>	7, 8
12.3	Morning	None	
19.7	Afternoon	None	
25.3	Afternoon	None	
26.5	Morning	None	
29.3	Afternoon	None	
32.3	Afternoon	None	
33.2	Afternoon	None	
39.8	Afternoon	None	
82.3	Afternoon	<i>Haminoea virescens</i>	13, 14, 16
		<i>Crucibulum spinosum</i>	9 ¹
		<i>Hermisenda crassicornis</i>	4 ²
90.7	Afternoon	<i>Hermisenda crassicornis</i>	3 ²
		unidentified crustacean	8
119.1	Afternoon	<i>Haminoea virescens</i>	11, 12, 13, 14 14, 14, 15, 16, 17
125.0	Afternoon	None	
130.2	Afternoon	<i>Haminoea virescens</i>	12, 12, 13
		<i>Crucibulum spinosum</i>	9

¹ defecated in the living state

² length of radula

and their distribution relative to each other. One area contained dense beds of eelgrass (7 m wide) and the other contained relatively sparse patches of eelgrass (12 m wide). The length of each area extended from the high tide level down to a depth at which visibility in the water was minimal – usually about 2 m. Sampling was carried out during one high tide, one intermediate tide, and 3 low tides.

In the study on location of prey, a wading pool 1 m in diameter was placed on the beach at the edge of the tide beneath the shadow of a pier. Sufficient sand was placed inside the pool to cover the bottom and the pool was filled to capacity with sea water. Temperature of the pool water was never more than 3°C warmer than the nearshore surface water temperature that ranged from 19 to 20°C. Various prey types were placed on the sand and guided by means of forceps to fit each distinct experimental design. The nudibranch *Hermisenda crassicornis* (Esch-

scholtz, 1831) and the tectibranch *Bulla gouldiana* were used in the majority of experiments because they were the most motile and easily guided species of prey. A specimen of *Navanax inermis* was next placed on the sand (taking care to place the animal well away from the trail so that it would encounter the trail “by chance” during its movements within the pool) and its movements observed and recorded. For each experimental arrangement, an average of 7 replications were recorded.

RESULTS

Very few *Navanax inermis* were collected within eelgrass beds. The great majority were found on undisturbed sandy-mud bottoms. The hard parts defecated by *N. inermis* (Table 1) revealed a predominance of *Haminoea virescens* in the diet. *Haminoea virescens* represented 75%

of the total number of prey passed through the guts of those specimens studied; *Hermisenda crassicornis* represented 8%; and *Teinostoma supravallatum* (Carpenter, 1864), *Crucibulum spinosum* (Sowerby, 1824), *N. inermis* and an unidentified crustacean comprised 17%. Particularly noteworthy is the record of no prey hard parts from *N. inermis* between the sizes of 12 and 82 g. The length of ingested *H. virescens* ranged from 5 to 17 mm. Prey *H.*

virescens of less than 8 mm were selectively eaten by 11 to 12 g *N. inermis*, while *H. virescens* of greater than 11 mm length were eaten only by *N. inermis* of greater than 82 g weight.

When all the data on the occurrence of prey in the 2 sampling areas (Figure 2) were added together, *Haminoea virescens* comprised 62%, *Phyllaplysia taylori* 20%, and *Nassarius tegula* 18% of the gastropods collected. The summation of data from Figure 2 was justified on the basis that *Navanax inermis* occurred randomly on sandy-mud bottoms throughout the study area and that the numbers of available *N. inermis* limited to any specific area were too few for the adequate analysis of gut contents.

Because sample sizes were small it was not possible to quantitatively assess population densities or describe the types of dispersion exhibited by each prey species. However, it appeared (Figure 2) that *Nassarius tegula* was strongly aggregated; *Phyllaplysia taylori* was weakly aggregated; and *Haminoea virescens* was uniformly dispersed. Both *N. tegula* and *P. taylori* were conspicuously absent from the 12 m area of sparse eelgrass.

During the present study a "searching" posture (with the body fully extended and the head occasionally making small sweeps) was observed consistently for each *Navanax inermis*, whether it had previously contacted a trail or not. When *N. inermis* detected the presence of a trail, the sweeping motion became much reduced, and the animal then followed the trail. The angle at which *N. inermis* made first contact with the mucus trail varied, and did not appear to affect its ability to initiate movement upon the trail. After *N. inermis* made initial contact with the prey, it moved its head from one side of the prey shell or body to the other side and then ingested it directly. Following ingestion of the prey, the *N. inermis* immediately resumed its "searching" posture.

The results of the specific experiments conducted on prey location are summarized in Table 2. *Hermisenda crassicornis* was used (Experiment 1) to describe a circular pathway. *Navanax inermis* made contact with the circular trail and followed it to the site of initial contact, whereupon it veered away. An alpha-shaped trail (Experiment 2) was made with *H. crassicornis*; *N. inermis* entered the trail at its origin and followed the trail to its end. The remaining experiments involved use of straight trails. In the first of these experiments (Experiments 3 and 4), the trail of a known prey type was interrupted and replaced by the trail of a different known prey type. In both experiments *N. inermis* did not veer away at the intersection of the 2 trails. If one known prey type was replaced at the end of its mucus trail by a different known prey type (Experiments 5 and 6), *N. inermis* followed the path and ingested the prey directly. However, when

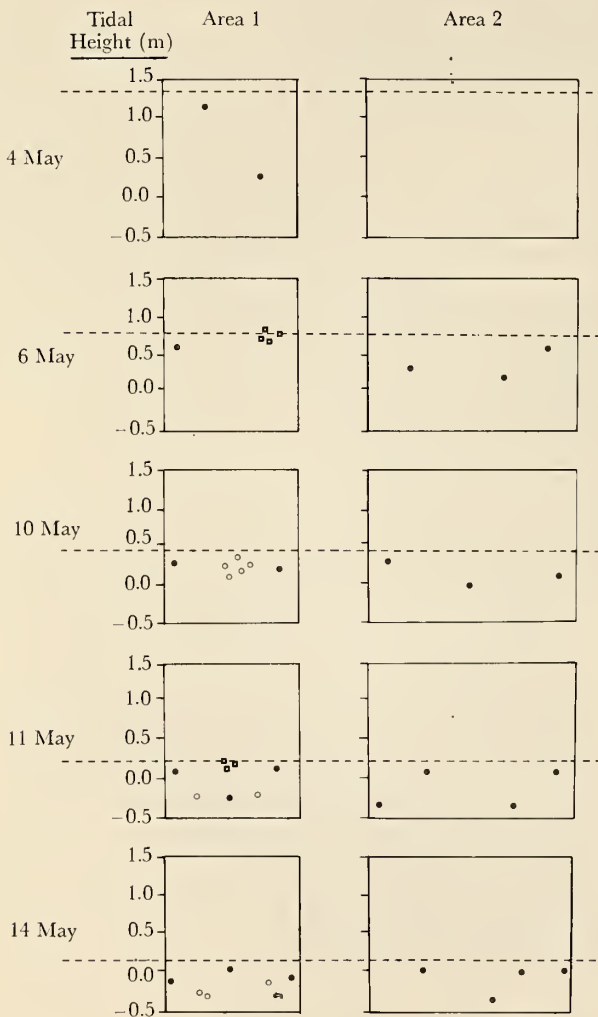


Figure 2

Occurrence of gastropods in sampling areas 1 and 2 at Balboa Island, Newport Bay. For each date the tidal height at the time of observation is indicated by the horizontal dashed line. Observed gastropods in the two areas include *Nassarius tegula* (□), *Phyllaplysia taylori* (○) and *Haminoea virescens* (●)

Table 2
Response of *Navanax inermis* to Gastropod Mucus Trails

Experiment Number	Experimental Design	Results	Number of Replicates
1	A circular mucus trail (30 to 40 cm diameter) made by <i>Hermisenda crassicornis</i>	<i>Navanax inermis</i> entered, followed the trail and exited at the point at which it first made contact with the trail	6
2	A mucus trail in an alpha (α) configuration (circular part 35 to 45 cm diameter) made by <i>Hermisenda crassicornis</i>	<i>Navanax inermis</i> entered one arm of the alpha configuration, and followed the trail through to the end, with no hesitancy or deviation at the intersection of the loop	6
3	A straight trail (50 to 60 cm), one-half consisting of mucus from <i>Bulla gouldiana</i> , and the other half from <i>Haminoea virescens</i>	<i>Navanax inermis</i> followed the entire trail without hesitancy at the point where the <i>Haminoea virescens</i> trail began	6
4	A straight trail (55 to 65 cm), one-half consisting of mucus from <i>Bulla gouldiana</i> , and the other half from <i>Hermisenda crassicornis</i>	<i>Navanax inermis</i> followed the entire trail without hesitancy at the point where the <i>Hermisenda crassicornis</i> trail began	7
5	A straight trail of <i>Bulla gouldiana</i> (25 to 40 cm) with <i>Haminoea virescens</i> placed at the end of the trail immediately before contact by <i>Navanax inermis</i>	<i>Navanax inermis</i> followed the trail and, upon completing the trail, immediately ingested the substituted <i>Haminoea virescens</i>	7
6	A straight trail of <i>Hermisenda crassicornis</i> (35 to 40 cm) with <i>Haminoea virescens</i> placed at the end of the trail immediately before contact by <i>Navanax inermis</i>	<i>Navanax inermis</i> followed the trail and, upon completing the trail, immediately ingested the substituted <i>Haminoea virescens</i>	6
7	A straight trail (50 to 60 cm), one-half consisting of mucus from <i>Hermisenda crassicornis</i> , and the other half from <i>Nassarius tegula</i>	<i>Navanax inermis</i> followed the <i>Hermisenda crassicornis</i> trail and veered away immediately after contacting the trail of <i>Nassarius tegula</i>	7
8	A straight trail of <i>Hermisenda crassicornis</i> (30 to 40 cm) with <i>Nassarius tegula</i> substituted immediately before contact by <i>Navanax inermis</i>	<i>Navanax inermis</i> followed the <i>Hermisenda crassicornis</i> trail and did not ingest the <i>Nassarius tegula</i> at the end of the trail	7
9	A straight trail of <i>Bulla gouldiana</i> (30 to 40 cm) with <i>Nassarius tegula</i> substituted immediately before contact by <i>Navanax inermis</i>	<i>Navanax inermis</i> followed the <i>Bulla gouldiana</i> trail and did not ingest <i>Nassarius tegula</i> at the end of the trail	7

the latter half of this mucus path was replaced with the mucus from the neogastropod *Nassarius tegula* (Experiment 7), *Navanax inermis* lost the trail at the point where it contacted the mucus of *Nassarius tegula*. Furthermore, *Navanax inermis* could not be induced into eating *Nassarius tegula* (Experiments 8 and 9) by placing *Nassarius tegula* at the end of a trail of a known prey type.

DISCUSSION

Haminoea virescens represented 62% of the total gastropod species present in the environment and 74% of the diet of *Navanax inermis*. Although *Phyllaplysia taylori*

and *Nassarius tegula* were relatively abundant in the field (20% and 18%, respectively, of the gastropods present), both of these species were absent from the diet of *N. inermis*. The absence of *Nassarius tegula* from the diet is predictive in light of the present experimental evidence on rejection by *N. inermis*. Additionally, the distinctive behavioral characteristics of *P. taylori* and *Nassarius tegula* would reduce the probability of their encounter in the field by *N. inermis*. *Phyllaplysia taylori* normally occurs (MACGINITIE & MACGINITIE, 1968) in beds of eelgrass. In the present study only small *N. inermis* were infrequently encountered in eelgrass. Species of *Nassarius* remain burrowed in bay bottoms until stimulated by distant chemoreceptive detection of decaying flesh when they will

rise to the surface and aggregate around the dead animal (KOHN, 1961). In the present study, *Nassarius tegula* was periodically observed in small groups of 4 or 5 individuals, either moving across the bay bottom or feeding on decaying fish. Thus, the aggregated distribution of *Nassarius tegula* decreases the probability of encounter in the field by *N. inermis*, whose movements during prey location appear to be random. In contrast to the aggregated distribution of *P. taylori* and *Nassarius tegula*, *H. virescens* appeared to be uniformly spaced (Figure 2) along the bottom. This spacing greatly enhances the probability of *N. inermis* meeting the mucus trail of an individual *H. virescens*. Thus, in addition to its abundance in the field, an important factor in favoring predation on *H. virescens* could be its optimal accessibility.

In the experiments on prey location, *Navanax inermis* responded positively to a combination of mucus trails from different known prey types. It did not follow the mucus trails of *Olivella biplicata*, *Conus californicus* (PAINE, 1963), or *Nassarius tegula* (as demonstrated in the present study). Indeed, *Navanax inermis* could not be induced to accept *Nassarius tegula* even if the mucus trail of it was preceded by that of an acceptable prey type or when *Nassarius tegula* was placed halfway within the mucus sheath at the end of a mucus trail made by *Haminoea virescens*. When *Nassarius tegula* was replaced by *H. virescens*, the latter was quickly ingested. Thus, not only was *Nassarius tegula* observed to be inaccessible to *Navanax inermis* in the field, it was not an acceptable prey. Whether this reaction represented chemoreceptive rejection or was simply a lack of response by *Navanax* toward the presence of *Nassarius tegula* is an area for future experimentation.

Navanax inermis did not exhibit any hesitancy in movement when following trails comprised of 2 different known prey types. Apparently, *N. inermis* will follow the mucus trail of opisthobranch prey without regard to the particular species involved in the interaction. If encountering overlapping trails from 2 known prey types in the field, this characteristic would confer the adaptive advantage on *N. inermis* of continuing to follow one mucus path rather than hesitating and possibly losing track of both trails.

The ability to utilize contact chemoreception in prey location makes *Navanax inermis* a highly efficient predator. The evolution of this chemoreceptive mechanism has resulted in the reduction of energy required for prey capture. The ability to differentiate acceptable opisthobranch prey from unacceptable prosobranch prey further reduces energy losses during prey location.

CONCLUSIONS

The carnivorous sea slug *Navanax inermis* exhibits distinctive prey selectivity and a unique mechanism for prey location. The diet of *N. inermis* occurring on sandy-mud bottoms is different from that previously reported from a sand-bottom bay and exposed rocky coastline. On sandy-mud bottoms *Haminoea virescens* is the most accessible prey type occurring in the environment as well as the most abundant prey type in the diet of *N. inermis*. Two potential species of prey (*Nassarius tegula* and *Phyllaplysia taylori*) were abundant in the field but were not accessible to *N. inermis* and were absent from its diet.

Navanax inermis utilizes contact chemoreception to locate and follow the mucus trails of its opisthobranch prey. In the field, mucus trails were made over sand by carefully guiding various gastropod prey through predetermined pathways. In every case when a prey type was used that was known to be a preferred prey species, *N. inermis* would follow the mucus trail, overtake, and ingest the prey. By replacing one prey type with another halfway through the trail, various combinations of mucus trails were obtained. *Navanax inermis* continued to follow a trail comprised of 2 different known prey types, but would not follow the last half of a trail if it was made by a gastropod other than a known prey type. The utilization of contact chemoreception in the location of acceptable prey is an important mechanism of energy conservation.

Literature Cited

- BRAAMS, W. G. & HANNIE F. M. GEELLEN
1953. The preference of some nudibranchs for certain coelenterates. Arch. néerl. Zool. 10 (3): 241-262
- KOHN, ALAN JACOBS
1959. The ecology of *Conus* in Hawaii. Ecol. Monogr. 29: 47-90
1961. Chemoreception in gastropod molluscs. Amer. Zool. 1: 291 to 308
- MACGINITIE, GEORGE EBER & NETTIE MACGINITIE
1949. Natural history of marine animals. McGraw-Hill Book Co., New York, N. Y. xii+473 pp.; 286 text figs.
- MARCUS, ERNST
1961. Opisthobranch mollusks from California. The Veliger 3 (Supplmt. 1): 1-85; pls. 1-10 (1 February 1961)
- PAINE, ROBERT TREAT
1963. Food recognition and predation on opisthobranchs by *Navanax inermis* (Gastropoda: Opisthobranchia). The Veliger 6 (1): 1-9; 1 plt.; 1 text fig. (1 July 1963)
1965. Natural history, limiting factors, and energetics of the opisthobranch *Navanax inermis*. Ecology 46 (5): 603-619; 9 text figs.
- RICKETTS, EDWARD F. & JACK CALVIN
1968. Between Pacific tides. Stanford Univ. Press, Stanford, Calif. v-xiii+3-502; 46 pls.
- ROBILLIARD, GORDON A.
1971. Predation by the nudibranch *Dirona albolineata* on three species of prosobranchs. Pacif. Sci. 25 (3): 429-435
- STEHOUWER, H.
1952. The preference of the slug *Aeolidia papillosa* (L.) for the sea anemone *Metridium senile* (L.). Arch. néerl. Zool. 10: 161-170